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Research Article

Temporal Dynamics of Roost Snags of Long-Legged Myotis in the Pacific Northwest, USA

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ABSTRACT Snags are used as roosting sites by many bats living in coniferous forests of western North America. Thus, providing sufficient numbers of snags both spatially and temporally in forested landscapes is critical to sustaining populations of these species. One aspect that remains poorly understood is length of time that roost snags persist on the landscape in a form suitable for use by bats. This information is critical for forest-planning efforts in ensuring long-term availability of snag resources on forested landscapes. We monitored condition of 339 snags used as roosting sites by long-legged myotis (*Myotis volans*) 1–5 years post-discovery from 2001 to 2006 across 6 watersheds in Washington, Oregon, and Idaho, USA. Persistence rates (i.e., probability a snag remains standing from year x to $x + 1$) of roost snags declined with year post-discovery in all study areas. Fir snags (*Abies* spp.) exhibited lower persistence rates than other conifer species. Data for the Washington area indicated only 4.3% of roost snags likely remain standing 10 years post-discovery, with half-lives of all snag species <3 roost-years. Model ranking of habitat models predicting fall year of roost snags revealed that snag condition models were the most parsimonious in all geographic locations. Roost snags larger in diameter, shorter in height, and with fewer branches on the bole were likely to persist for more years. These data indicate that snags used as roosts by long-legged myotis are suitable as roosting sites for only a few years before falling. We recommend management policies for coniferous forests in the Pacific Northwest, USA, that promote sufficient leave-trees in set-aside areas to provide for future suitable, large-diameter snags for bats in managed, forested landscapes. © 2012 The Wildlife Society.

KEY WORDS conifers, fall rate, Idaho, *Myotis volans*, Oregon, roosting sites, snags, Washington.

Snags promote healthy forests by supporting plant and animal biodiversity, and by contributing, through the decay process, to energy flow and nutrient cycling pathways (Molina and White 2007). In forests of the Pacific Northwest, USA, multiple species of bats depend on snags for habitat (Rancourt et al. 2005, Baker and Lacki 2006, Lacki and Baker 2007, Arnett and Hayes 2009). Thus, providing sufficient numbers of snags both spatially and temporally on forested landscapes is critical to sustaining populations of bat species in this region. Studies have documented that snags taller in height, larger in diameter, and possessing ample cavities and exfoliating bark are preferred by forest-dwelling bats (Lacki and Baker 2003, Kalcounis-Rüppell et al. 2005, Barclay and Kurta 2007). One facet of the dynamics of bat roost snags that has not received attention, however, is the temporal stability of this resource and how it affects use by roosting bats.

Bats use snags for night- and day-roosting, and for shelter, resting, feeding, and rearing pups (Kunz and Lumsden

2003). Bark and cavity-roosting bats switch roosts frequently, using multiple snags across the landscape during a single summer season (Barclay and Kurta 2007). Bats choose roosts for a variety of reasons (Lewis 1995), including closer proximity to food resources (Kunz 1974, Kunz and Anthony 1996, Adams 1997) and drinking water (Adams and Hayes 2008), and to avoid excessive parasite loads in infected roosts (ter Hofstede and Fenton 2005, Lourenço and Palmeirim 2007). Bats form expanded social groups that move among roosts, maintaining social cohesion among members of the group (Kerth and König 1999, Willis and Brigham 2004, Garroway and Broders 2007, Patriquin et al. 2010), and exhibiting loyalty to roosting areas (Ormsbee and McComb 1998, O'Donnell 2000, Kerth et al. 2001).

Reuse of tree roosts has been demonstrated for forest-dwelling bats in European forests, with select tree cavities reused up to 16 years (Lučan et al. 2009). In aspen forests of Saskatchewan, Canada, big-brown bats (*Eptesicus fuscus*) reused cavities in live trees up to 10 years, with 3-year periods of reuse most common (Willis et al. 2003). Conversely, California bats (*Myotis californicus*) reused most roost snags up to 5 years, but the size of roosting colonies declined with time, leading the authors to hypothesize that suitability of

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roost snags of bats declines more quickly than the available population of snags across forested landscapes (Barclay and Brigham 2001). These patterns suggest that temporal accessibility of roost snags influences survival of forest-dwelling bats, and a better understanding of roost snag dynamics, particularly longevity, is needed to ensure adequate habitat for these bats in northern-temperate zone forests.

Studies have examined snag dynamics in coniferous forests of western North America (Morrison and Raphael 1993, Bagne et al. 2008, Kennedy et al. 2010), including estimation of fall rates (DeLong et al. 2008), persistence rates (Russell et al. 2006), and survivorship probabilities among years (Angers et al. 2010). Habitat characteristics of snags demonstrate that snags shorter in height and lacking tops, larger in diameter and in earlier stages of decay persist longer on the landscape (Cline et al. 1980, Morrison and Raphael 1993, Everett et al. 1999); however, whether these rates and habitat conditions are also representative of roost snags of bats remains unclear. Because bats preferentially select snags for roosting with features different from that of the available population of snags (Lacki and Baker 2003, Kalcounis-Rüppell et al. 2005), the structural configuration, state of decay, and stand and landscape positions of roost snags may result in differences in fall rates and survivorship patterns from that of the population of available snags. Therefore, we tested Barclay and Brigham's (2001) hypothesis that roost snags of bats decline more rapidly than random snags by tracking the survivorship of roost snags of long-legged myotis (*Myotis volans*) in Washington, Oregon, and Idaho, USA, from 2001 to 2006, and comparing our findings with the published literature on snag dynamics in coniferous forests of western North America. We chose long-legged myotis as the study species because it is widespread throughout forests of the Pacific Northwest, and it remains a species of concern due to a poor understanding of its ecology and habitat requirements (Harvey et al. 1999, Adams 2003).

STUDY AREA

Our study encompassed 2 mountain ranges, the east side of the Cascade Range (Washington and Oregon) and the western side of the Rocky Mountains (Idaho). We conducted our study in Kittitas and Yakima counties in south-central Washington, in Klamath and Lake counties in south-central Oregon, and in Clearwater and Latah counties in north-central Idaho. We chose 2 watersheds in each area for sampling: Rock Creek and Oak Creek drainages on the Okanogan-Wenatchee National Forest, Washington; Pole Creek and Sprague River drainages on the Fremont-Winema National Forest, Oregon; and Elk Creek and Long Meadow Creek drainages on the Clearwater National Forest, Idaho. All study areas were >500 km apart.

The physiography of the Washington area was characterized by andesite and basalt flows with ridge crests separated by deep valleys (Franklin and Dyrness 1988). Elevations in the Washington drainages ranged from 760 m to 1,400 m. The physiography of the Oregon area was comprised of Miocene to recent basalt flows, pyroclastics, and alluvium

deposits overlying fault-block mountain topography (Franklin and Dyrness 1988). Elevations in the Oregon drainages ranged from 1,450 m to 2,000 m. Both areas possessed coarse-textured sandy soils and experienced dry summers (<15 mm precipitation/month) and winters with heavy snowfall (>2.5 m/yr; Franklin and Dyrness 1988). The topography of the Idaho area was also diverse with much local variation. Elevations in the Idaho drainages ranged from 480 m to 1,410 m. Climate in the Idaho area was mild and dry, with average daily temperatures ranging from 6.72° C (Jun) to 25.5° C (Aug), and a monthly summer precipitation averaging 39 mm (Western Regional Climate Center 2011).

Dominant tree species in the Washington area were ponderosa pine (*Pinus ponderosa*), grand fir (*Abies grandis*), and Douglas-fir (*Pseudotsuga menziesii*). Dominant tree species in Oregon were ponderosa pine, white fir (*A. concolor*), western juniper (*Juniperus occidentalis*), and incense cedar (*Libocedrus decurrens*). Dominant tree species in Idaho included grand fir, western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), Douglas-fir, and western larch (*Larix occidentalis*). Land ownership and management were diverse in all 3 study areas, with private industrial forested lands interspersed within the matrix of national forest lands. Thus, these landscapes were managed for timber production and forests were a mix of stand ages, including even- and uneven-aged stands created by a variety of silvicultural treatments.

METHODS

We located roost snags of long-legged myotis by radiotracking bats to roosting sites during daylight hours. We radio-tracked bats in Washington in 2001 and 2002, in Oregon in 2003 and 2006, and in Idaho in 2004 and 2005. A majority of bats we radiotracked (>90%) were adult females, but some roosts included in analyses also periodically housed radio-tagged male bats. Details of capture, handling, tagging, and radiotracking of bats are published elsewhere (Washington and Oregon areas: Baker and Lacki 2006; Idaho area: Johnson et al. 2007). The Institutional Animal Care and Use Committee at the University of Kentucky (IACUC no. 00219A2001) approved all animal-handling methods associated with our study.

We measured habitat characteristics at each roost snag in the year of discovery. For each roost snag, we recorded location and altitude using digital topographic maps and Global Positioning Systems (GPS). We qualitatively assessed branches remaining on the bole (%) and canopy closure of the surrounding stand (%). We estimated height of roost snags (m) with a clinometer, and measured diameter of stems in cm at 1.5 m aboveground using a diameter tape. We measured stand-level variables inside 20-m radius plots around roost snags (Ormsbee and McComb 1998). We counted number of stems, live and dead, ≥10 cm in diameter to calculate live tree density (*n*/ha) and snag density (*n*/ha), respectively. We measured slope (%) using a clinometer.

We derived landscape-level habitat characteristics using GPS coordinates of roost snags coupled with Geographic

Information Systems databases provided by the United States Department of Agriculture, Forest Service located at the Okanogan-Wenatchee, Fremont-Winema, and Clearwater National Forests. From these data, we obtained estimates of elevation (m) and the number of stands within a 250-m radius of the snag (n).

Using GPS coordinates, we monitored roost snags in periodic years to assess their condition and determine whether they remained standing or had fallen down and, thus, no longer served as suitable bat roosts. In the Washington area, we monitored roost snags recorded in the 2001 cohort in 2002, 2004, and 2006, or 1 year, 3 years, and 5 years post-discovery. We monitored roost snags recorded in the 2002 cohort in 2004 and 2006, or 2 years and 4 years post-discovery. In the Oregon area, we monitored roost snags recorded in the 2003 cohort in 2004 and 2006, or 1 year and 3 years post-discovery. In the Idaho area, we monitored roost snags recorded in the 2004 cohort in 2005 and 2006, or 1 year and 2 years post-discovery. We monitored roost snags recorded in the 2005 cohort in 2006 or 1 year post-discovery. Roost snags that we could not re-locate ($n = 30$) or were felled in a logging operation ($n = 8$) were omitted from analyses.

We calculated persistence rates (i.e., probability a snag remains standing from year x to $x + 1$; Russell et al. 2006) for each area-year combination and for tree species by area-year combination. For the Washington area, we multiplied persistence rates across cohorts of roost snags to generate percent survivorship (proportion of snags still standing) by roost-years (years standing post-discovery of use by roosting bats; Everett et al. 1999), for ponderosa pine, grand fir, and Douglas-fir. We used persistence rate for 5 roost-years to project survivorship of a snag species out to 10 roost-years. We generated half-lives (i.e., the years required for half of the snags to have fallen to the ground; Angers et al. 2010) for ponderosa pine, grand fir, and Douglas-fir roost snags in the Washington area.

We used multiple linear regression coupled with Akaike's Information Criterion (AIC) model rankings (Burnham and Anderson 2002) to identify the most parsimonious model for predicting fall year of roost snags from habitat characteristics associated with roost snags. We derived 3 a priori habitat models and tested the suitability of these models across study areas. We used AIC scores adjusted for small sample size (AIC_c) to identify the most parsimonious models in each study area. We derived models to reflect mechanistic hypotheses for explaining patterns in snag fall rates (Ober and Hayes 2008, Lacki et al. 2010). Predictor variables in the model describing roost snag condition and state of decay (snag condition model) included roost snag height (m), roost snag diameter (cm), and percent of branches remaining on the roost snag (%). The model describing the ability of forest stands to protect stability of roost snags (stand structure model) included snag density (n/ha), live tree density (n/ha), and canopy closure (%). The model describing the effect of landscape position on stability of roost snags (landscape exposure model) included slope (%), elevation (m), and forest fragmentation (no. stands within 250-m radius of

snag). We used AIC_c differences relative to the smallest AIC_c value (ΔAIC_c) and Akaike weights (w_i) to assess the suitability of habitat models (Burnham and Anderson 2002, Arnold 2010). For models with strong support, we examined parameter estimates and associated standard errors to identify 85% confidence intervals that did not overlap zero (Cox et al. 2008).

RESULTS

We successfully monitored 301 (88.8%; $n = 339$) roost snags of long-legged myotis. Overall, persistence rates declined with increasing roost-years across study areas (Table 1). Roost snags in Washington showed a lower persistence rate 1-year post-discovery than did roost snags in Oregon and Idaho. Persistence rates varied among snag species, with firs (*Abies* spp.) showing lower persistence rates across most roost-years post-discovery than other snag species, regardless of area (Table 1). Persistence rates of ponderosa pine snags in Washington varied 3–5 years post-discovery, and an explanation for the drop in persistence rate 4 years post-discovery is unclear.

Survivorship of snag species in Washington demonstrated similar relationships for grand fir, ponderosa pine, and Douglas-fir, especially after the first year of sampling (Fig. 1). Half-lives of all snag species were <3 roost-years (grand fir = 2.75 yr, ponderosa pine = 2.64 yr, Douglas-fir = 2.5 yr). Estimates of percentage of snags still standing 10 years post-discovery were highest for ponderosa pine (6.8%), slightly less for Douglas-fir (5.3%), and lowest for grand fir (0.9%).

Rankings of habitat models of snag fall-year showed snag condition models to be most parsimonious in all 3 study areas (Table 2). Parameter estimates for snag diameter were significant ($P < 0.15$) in 2 of 3 study areas and indicated that roost snags greater in diameter persisted for longer periods of time than smaller-diameter roost snags (Table 3). Height of roost snags was influential in predicting fall-year in Oregon, with roost snags 10 m tall persisting for a year longer than

Table 1. Persistence rates of snag species used as roosts by long-legged myotis in Washington, Oregon, and Idaho, USA, 2001–2006.

| | Persistence rate post-discovery | | | | |
|------------------------------|---------------------------------|-------|-------|-------|-------|
| | 1 yr | 2 yr | 3 yr | 4 yr | 5 yr |
| Washington ($n = 103$) | | | | | |
| <i>Abies grandis</i> | 0.632 | 0.76 | 0.777 | 0.678 | 0.556 |
| <i>Pinus ponderosa</i> | 0.8 | 0.786 | 0.762 | 0.4 | 0.842 |
| <i>Pseudotsuga menziesii</i> | 1.0 | 0.6 | 0.667 | 0.75 | 0.75 |
| All snags | 0.763 | 0.75 | 0.744 | 0.596 | 0.735 |
| Oregon ($n = 50$) | | | | | |
| <i>Abies concolor</i> | 0.615 | | 0.556 | | |
| <i>Pinus ponderosa</i> | 0.914 | | 0.632 | | |
| All snags | 0.84 | | 0.633 | | |
| Idaho ($n = 148$) | | | | | |
| <i>Abies grandis</i> | 0.763 | 0.714 | | | |
| <i>Larix occidentalis</i> | 1.0 | 1.0 | | | |
| <i>Pinus monticola</i> | 0.833 | 1.0 | | | |
| <i>Pseudotsuga menziesii</i> | 0.954 | 0.733 | | | |
| <i>Thuja plicata</i> | 0.857 | 1.0 | | | |
| All snags | 0.851 | 0.797 | | | |

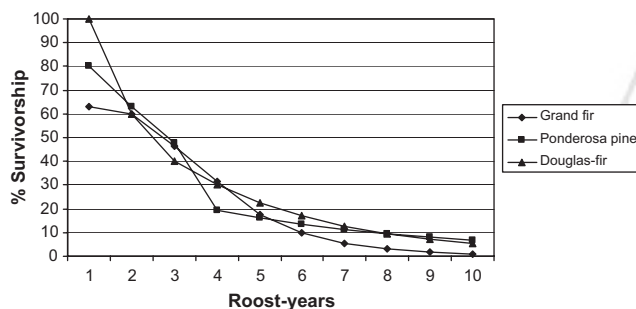


Figure 1. Survivorship (%) of roost snags by roost-years (years post-discovery of use by roosting bats) for species used as roosts by long-legged myotis in Washington, USA.

roost snags 40 m in height. Percent of branches remaining predicted fall-year of roost snags in Washington, with roost snags lacking branches standing for approximately 4.23 years, whereas roost snags retaining all branches on the bole fell within 3.2 years post-discovery.

Model rankings indicated moderate support for the stand structure model in Washington and stand structure and landscape exposure models in Idaho (Table 2). However, only live tree density significantly predicted roost snag fall-rates ($\beta = 0.002$, $SE = 0.001$, $P < 0.15$), with density of forested stands in Washington directly related to persistence times of roost snags.

DISCUSSION

Survivorship curves for conifer species show considerable variation, with most species in boreal forests exhibiting reverse sigmoid functions (Angers et al. 2010). We found limited variation in shape of survivorship curves of bat roost snags across conifer species in Washington, with grand fir, ponderosa pine, and Douglas-fir all exhibiting similar declines in survivorship after year 1. Grand fir possessed

the longest half-life of any snag species, but because of declines in persistence rates over time was the snag species least likely to remain standing (<1%) 10 years post-discovery. This is in contrast to data for snags in California that found fir (*Abies* spp.) to decay more slowly than pine (*Pinus* spp.) species (Morrison and Raphael 1993). Russell et al. (2006) found persistence of Douglas-fir snags to exceed that of ponderosa pine, whereas our data indicated longer half-lives and a greater percentage still standing 10 years post-discovery for roost snags of ponderosa pine than for Douglas-fir. Based on our results, we hypothesize that ponderosa pine snags selected by long-legged myotis for roosting are a more temporally predictable resource than either grand fir or Douglas-fir in Pacific Northwest forests.

High fall rates appeared to occur earlier for bat roost snags than for populations of conifer snags in the east Cascades of Washington (Everett et al. 1999), the western Rocky Mountains in Idaho (Russell et al. 2006), and boreal coniferous forests of Canada (DeLong et al. 2008, Angers et al. 2010). Half-lives of snags of ponderosa pine (7–10 yr) were less than Douglas-fir (12–16 yr) in Idaho (Russell et al. 2006), and half-lives of conifer snags in boreal forests ranged from >10 years to <30 years for the species examined (Angers et al. 2010). In all cases, half-lives of snags reported exceed those observed for bat roost snags in our study, regardless of species; all half-lives in our study were <3 roost-years. Data for conifer snags in Sierra Nevada, California, demonstrated most snags in advanced stages of decay fell within 5 years (Morrison and Raphael 1993). This latter finding is more consistent with patterns in survival observed for roost snags in our study, suggesting, perhaps, that long-legged myotis choose snags in later stages of decay relative to the available population of snags on the landscape.

Comparison of habitat models for predicting fall year demonstrated the snag condition model to be most parsimonious in all study areas. We found limited evidence in

Table 2. Akaike's Information Criterion scores (AIC_c), difference in AIC_c values (ΔAIC_c), Akaike weights (w_i), and number of parameters (K) for linear regression models of fall-year by habitat characteristics for snags used as roosts by long-legged myotis in Washington, Oregon, and Idaho, USA, 2001–2006.

| State | Model | AIC_c | ΔAIC_c | w_i | K |
|--------------------------|--------------------|---------|----------------|-------|-----|
| Washington ($n = 114$) | Snag condition | 171.28 | 0 | 0.712 | 4 |
| | Stand structure | 173.74 | 2.46 | 0.208 | 4 |
| | Landscape exposure | 175.64 | 4.36 | 0.08 | 4 |
| Oregon ($n = 57$) | Snag condition | 47.94 | 0 | 0.864 | 4 |
| | Landscape exposure | 52.08 | 4.14 | 0.109 | 4 |
| | Stand structure | 54.89 | 6.95 | 0.027 | 4 |
| Idaho ($n = 144$) | Snag condition | −99.83 | 0 | 0.517 | 4 |
| | Landscape exposure | −98.45 | 1.38 | 0.259 | 4 |
| | Stand structure | −98.15 | 1.68 | 0.223 | 4 |

Table 3. Parameter estimates (β) and standard errors (SE) for predictor variables of the most parsimonious model of snag fall rates by location, 2001–2006. Parameters estimates indicated by an asterisk (*) have 85% confidence intervals that do not overlap zero.

| Habitat characteristic | Parameter estimate (β) \pm SE | | |
|------------------------|---|---------------------|--------------------|
| | Washington | Oregon | Idaho |
| Snag height (m) | −0.004 \pm 0.031 | −0.031 \pm 0.021* | −0.004 \pm 0.005 |
| Snag diameter (cm) | 0.018 \pm 0.009* | 0.028 \pm 0.01* | 0.004 \pm 0.003 |
| Branches remaining (%) | −1.009 \pm 0.587* | 0.382 \pm 0.686 | −0.207 \pm 0.198 |

support of stand structure and landscape position models for predicting fall year of bat roost snags. Thus, persistence of roost snags of long-legged myotis appeared to be most influenced by the snag itself and not surrounding habitat conditions. The effect of diameter on longevity of snags is well documented (Cline et al. 1980, Morrison and Raphael 1993, Everett et al. 1999, Garber et al. 2005), and our models corroborated this for roost snags. We found roost snags in an earlier state of decay, based on branches remaining, to not persist as long as snags with clean boles and, presumably, in a more advanced stage of decay. This was not consistent with findings for conifer snags elsewhere (Morrison and Raphael 1993). However, we also found evidence in the Oregon snag population of snag roosts shorter in height surviving for a longer period of time. This latter outcome is in agreement with patterns predicting snag persistence (Morrison and Raphael 1993).

Historical patterns in forest management on the east-side of the Cascades have resulted in increased tree densities in forests of this region (Agee and Edmonds 1992, Covington et al. 1994, Lehmkuhl et al. 1994). We found stand density to affect longevity of roost snags in the Washington area. Regardless, it remains unclear if the overall increase in tree density in this region indirectly benefits standing snags by slowing fall rates. Others have demonstrated increased snag longevity in stands of larger basal areas (Chambers and Mast 2005).

Future management of snags in forests of the Pacific Northwest will be inextricably linked to policies addressing disturbance regimes to sustain biodiversity and the need to reduce fuel loads, especially in seasonally dry forests (Odion and Sarr 2007, Boerner et al. 2008). Impacting this will likely be climate change bringing increased drought and enhanced tree mortality (Allen et al. 2010, Latta et al. 2010, Parks and Bernier 2010), further altering snag dynamics, including roost snags of forest-dwelling bats. Evidence suggests that past and present forest management in coastal Oregon has not sustained legacy dead wood structures at historic levels (Kennedy et al. 2010), and that benefits from existing policies to retain live (green) trees in forests of the Pacific Northwest are likely insufficient to support the full range of biodiversity in this region (Aubry et al. 2009). Use of thinning coupled with prescribed fire to sustain or increase snag abundance shows promise, but results of field studies are equivocal (Bagne et al. 2008, Harrod et al. 2009, Hessburg et al. 2010, van Mantgem et al. 2011).

We believe our findings support the hypothesis of Barclay and Brigham (2001) that suitability of roost snags of bats deteriorate more rapidly than the available population of snags in forested landscapes. We found half-lives of roost snags to be <3 roost-years, much shorter than published values for half-lives of snags of multiple species of conifers (Russell et al. 2006, Angers et al. 2010), and our overall average of roost snag persistence 10 years post-discovery across snag species was only 4.3%. Thus, replenishment of snags suitable for long-legged myotis on an annual basis is likely needed to ensure adequate habitat of this bat species, especially given the frequency of roost switching within years

shown by many bats (Lewis 1995, Barclay and Kurta 2007) and the short-term reuse of tree roosts among years by bats (Barclay and Brigham 2001, Willis et al. 2003, Lučan et al. 2009).

MANAGEMENT IMPLICATIONS

Results of our study indicate that most roost snags of bats in coniferous forests are not temporally stable and, thus, do not persist for very long periods of time. This outcome suggests that continued and regular replenishment of snags suitable to roosting bats is imperative if current population levels of bats are to be maintained or enhanced. This will be a challenging problem to solve, given the geographic variability in choice of snags for roosting both within and among species of bats in the Pacific Northwest region (Arnett and Hayes 2009, Lacki et al. 2010). We support management policies for coniferous forests in the Pacific Northwest, USA, that provide snags suitable for bats following future rotation harvests, especially when determining the periodicity, size, and extent of leave trees in set-aside areas across forested landscapes.

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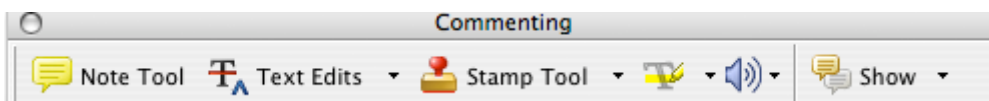
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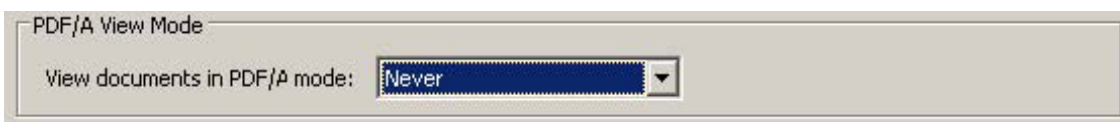


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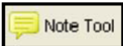
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